GENESIS OF THE ACTINOCRINIDÆ.

BY CHARLES R. KEYES.

THE crinoids belonging to the family Actinocrinidæ reached their greatest development and expansion during the lower Carboniferous period. In the American rocks the variety and number of these forms is indeed remarkable, perhaps nowhere equaled in any other age or region.

As regards the distribution of the group in time and space, and the phylogenetic history of the camarate forms in general, many pregnant suggestions have recently been offered by certain terranes in the Mississippi valley. But until quite lately attention has been turned in other directions than towards the solving of these problems; to the purely geologic considerations, and to the description of species. That such a large number of specific and higher terms should have been proposed, many of which are now regarded as invalid, is not surprising when it is remembered that serial comparisons were made only in exceptional cases, and that most of the forms show great variation, even now often offering more or less difficulty in definitely limiting the several sections. More recently efforts have been turned towards the structural features of the different groups, with most gratifying results towards a better understanding of the class. For a long time previous the lack of a sufficient variety and quantity of well-preserved examples of the occurring species had greatly embarrassed all efforts of this kind; and in many cases had led to very erroneous conclusions concerning the real structure of various parts of the skeletal arrangement. Late finds, however, have in great measure removed many of the difficulties that earlier would have very much hindered any attempts towards a satisfactory solution of the two questions already alluded to. They have also supplied enough additional data to render profitable the consideration anew of the entire stratigraphy of the Carboniferous rocks of the broad continental interior, with the

manifest result of a much better defined subdivision of the series than that now existing.

Geologic Distribution of the Actinocrinidæ.—More than three-fourths of the total number of genera of Actinocrinidæ are represented in America, distributed in time as shown in the accompanying chart, the relative expansion of each genus being also indicated. As compared with the ages preceding, the lower Carboniferous is here greatly exaggerated in order to show more clearly the relationship of the several zoological groups, for it was during this time that the greatest diversity of form, structure and general ornamentation occurred; in fact it was the culminating period of crinoidal life in America. Continuous lines are drawn where the record is complete and the transitions fully shown, while the dotted lines indicate the relation of the different types according to the evidence at present known, and probably coincide very closely with the real courses of divergence. The scheme is, then, to represent in a graphic way the relationship of the genera as now understood, rather than to construct a genealogical tree, with which attempts of this kind are often confounded. In the present instance some of the earlier, more generalized forms have not as yet been made known. There are also good grounds for believing that some of the generic types are considerably older than actual observation shows. In other groups, more particularly, there is abundant evidence pointing to a much higher antiquity of the leading generic types than is generally supposed. This is especially true of many widely distributed living organisms whose ancestry has lately proved to be very ancient.

Elements of Classification.—The most generalized type of the family Actinocrinidæ has dorsally a single ring of basal plates, three in number and of equal size, succeeded by a second circle of subequal pieces, six in number—the five radial and the primary anal plates. As in all camarate crinoids, the brachials for a considerable distance are incorporated into the calyx by means of interradial ossioles, and in the free portion of the rays they are biserial and closely interlocking. Ventrally five orals can, with a few exceptions, be made out; they are usually sur-

rounded by a greater or less number of smaller pieces. The anal aperture may be a simple opening immediately back of the orals, or at the end of a long ventral tube.

The fundamental modifications in the arrangement of the various plates give trustworthy criteria for the basis of genera; while the ornamentation, relative size and shape of the calyx ossicles form very satisfactory features for the distinction of species. The taxonomic values attached by different paleontologists to the various characters are not the same. This difference of interpretation, however, appears to arise largely from inattention to the ontogenetic history of the living forms of the class. But this diversity of opinion, happily, is rapidly lessening, with the prospect of a speedy agreement, at least in the main features, as to the relative worth of the separate structures in classification.

General Morphological Changes. — Before passing, however, to morphological details, it may be well to call attention to some widely-spread variations recorded. Briefly summing up, then, the statements recently[1] made in a general consideration of the most marked anatomical features displayed by the Carboniferous crinoids of the Mississippi basin, it may be said that these organisms, from the beginning of the lower carboniferous to the close of the Keokuk, showed: (1) a wonderful and extremely varied development of different structural characters; (2) a constant increase in size and massiveness of test; (3) a peculiar change in ornamentation, which, from the delicate style of the earlier forms, gradually grew more and more bold and rugged; and (4) many curious modifications in minor particulars.

These striking and wide-spread phenomena point to very decided changes in surroundings, such as might have resulted from a gradual decrease in the depth of the sea, a slight diminution, in the density of the water and the introduction of fine sediment in consequence of the nearer proximity to the drainage courses of the young continent, or marked alterations in the coastal contour of the neighboring mainland. There probably were acting also numerous other though less apparent influences. Indeed, these suggestions find substantiation in the stratigraphy

[1] Keyes: Carb. Echin. Mississippi Basin, *Am. Jour. Sci.*, Sept., 1889.

of the region, which gives every reason to believe that the changes went on quietly, yet at a rather rapid rate. The great abundance of individuals at this time may be due, in part at least, to the withdrawal of their more motile enemies because of the unsuitable physical impositions already mentioned. The comparatively rapid changes of environment thus imposed would force rapid modifications in the structure of the various individuals in order to secure a more perfect adaptation to the new conditions. And when these physical changes went on with still greater rapidity structural adjustment was unable to keep pace, and soon ended in the extinction of the group. The unfavorable conditions at a somewhat later period are further shown in the neighboring districts where a few types still persisted, small, depauperate and few in numbers.

Generic Considerations.—The Actinocrinoids are first known in the upper Silurian. They early showed signs of departure from the primitive form; and developed chiefly along two divergent lines. The one group continued to the Burlington with but slight tendencies to modification in general structure; the other soon broke up into a number of more or less well-marked sections, each of which rapidly expanded into new generic types, until about the close of the Keokuk, where, with a single exception, they became extinct. The present account will therefore make mention of the following groups as comprising the Actinocrinidæ: Periechocrinus, Megistocrinus, Amphoracrinus, Alloprosallocrinus, Agaricocrinus, Dorycrinus, Gennæocrinus, Eretmocrinus, Batocrinus, Actinocrinus, Teleiocrinus, Physetocrinus, Strotocrinus and Steganocrinus.

The general structure of the forms has already been alluded to, but some minor anatomical points in various genera may require further consideration. The first of the sections above referred to includes only two types—Periechocrinus and Megistocrinus. These genera differ from the other members of the family chiefly in the relatively large calyx, rather small branching arms, the large number of interradial plates, and in the structure of the ventral surface. In Periechocrinus the plates are smooth and thin; in Megistocrinus rather thick and more or less highly or-

amented. The anal interradius has three ossicles in the second tier, with many smaller pieces in the succeeding rows.

Amphoracrinus, in the general construction of the calyx, closely approaches some forms of Agaricocrinus, but its arms are very different, resembling more those of the preceding group. There are also other important distinctions. The earliest Agaricocrinus appears in the Kinderhook. At the beginning of the Keokuk a curious differentiation in some of the forms took place, giving rise to Alloprosallocrinus, of which but a single species is as yet known. The genus first mentioned is characterized by the flattened or concave dorsal region of the calyx, the free arms being given off low down on the margin of the basal plane. The rays are somewhat separated, especially on the posterior side, where a vertical row of anal plates is very noticeable. Ventrally, the calyx is greatly protuberant, and sometimes inflated not unlike that in Amphoracrinus.

Dorycrinus is the direct lineal successor of Gennæocrinus, from which it should, perhaps, not be separated generically. The anal structure links it closely with Agaricocrinus. It differs, however, in having the general arrangement of the calyx more like Batocrinus, and in a less massive arm structure. The long spines, so conspicuous on the ventral plates of some species, seem to be merely greatly exaggerated developments, homologous with the large nodosites on similar plates in Agaricocrinus.

Extreme forms of Eretmocrinus differ from those of Batocrinus principally in the long, lanceolate arms and inflated ventral parts. But the gradations are very complete, and it is often difficult to separate the forms of the two groups. In Batocrinus, the long anal tube, like that of the typical form of the family, is very prominent. The arms are short; the plates in the second tier of the anal interradius three in number, and the orals large and well defined.

Actinocrinus and the genera following have only two pieces in the second anal tier. In the leading genus two rather well-defined sections are recognized: one with the arms equi-distant around the margin of the calyx; the others with the arms in clusters, imparting a strongly quinquelobate symmetry. The

small number of brachials below the free arms is also very noticeable when compared with the four groups yet to be considered. Teleiocrinus departs from the type just mentioned in having a greater number of the lower brachials incorporated into the calyx, and forming a more or less pronounced decagonal rim just above those of the second order. In this respect it approaches somewhat towards Strotocrinus, but the latter has a very different ventral structure. Physetocrinus and Strotocrinus both differ from Actinocrinus in the structure of the ventral side, while the anal opening is a simple aperture in the test. The first of these types has the ventral portions of the calyx greatly elevated; the second nearly flat, while the rim is enormously developed, and the terminal free arms are not given off until the twelfth to fifteenth order of brachials. The calyx of Steganocrinus is most like that of the lobed section of Actinocrinus, but the radial extensions are most remarkable, and give rise to a very large number of free arms.

Geologic Development.—Inasmuch as the different phases passed through during the known existence of several of the genera mentioned have already been referred to elsewhere,[2] it is hardly necessary to take up here each group sepapately. It will suffice simply to consider somewhat in detail the geologic history of one of the leading generic types,—Actinocrinus,—which will also indicate the general course of development pursued by the other members of the family.

As yet the genus Actinocrinus is not known before the earliest part of the Lower Carboniferous—the Kinderhook. The forms from this horizon thus far discovered have all a more or less globular calyx, with the arms equidistantly distributed. The ornamentation has already assumed two very distinct phases. In the one, delicate ridges or small confluent nodes pass from the central portion of each dorsal plate of the calyx to the center of adjoining ossicles; in the other, the ridges are very inconspicuous, and the plates are strongly convex on the outer surface. These two styles of sculpturing continue during the existence of the group; but the first gradually loses its identity, while the second

[2] Wachsmuth and Springer, Proc. Acad. Nat. Sci., Phila., 1878.

becomes greatly intensified. In the earlier species the free arms are slender, growing much stouter in the Burlington and Keokuk, and in the latter often also branching one or more times. This development is accompanied by an increasing massiveness of the calyx plates and a change of the simple convexity of the ossicles into great, rude nodosities. Another marked feature is the tendency for the rays to separate from one another above the second brachials, forming prominent radial extensions before giving off the free arms. At the same time the interradial areas become somewhat more depressed. The quinquelobate calyx is thus produced; the form upon which the genus was was founded. In general it may be said that the earlier forms were of small size, delicately constructed and ornamented, and that they gradually became very much larger and more massive, with a rough, rugged ornamentation.

The more striking points in the development of the anatomical features in Actinocrinus, as here briefly traced, apply to the other genera here mentioned, and also to the members of other related families. Besides, Dorycrinus developed huge vertebral spines; Batocrinus, an immense disk-shaped calyx; Eretmocrinust broad lanceolate arms; Strotocrinus, a large rim stretching out laterally from above the tertiary brachials; and Steganocrinus, monstrous radial extensions, from which the free arm sprung.

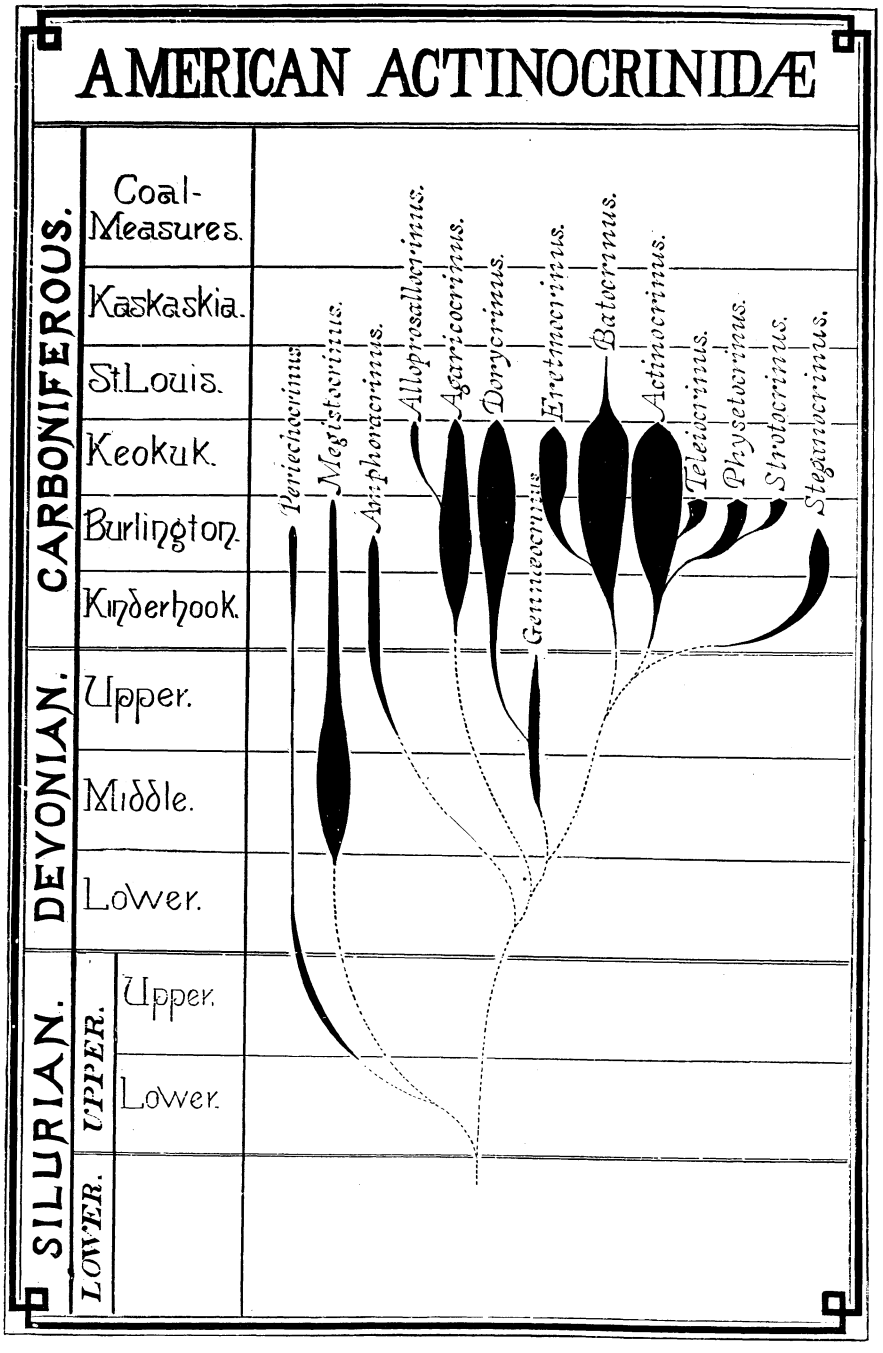
Generic Relationships.—As previously stated, Periechocrinus and Megistocrinus are closely related, but differ considerably from other members of the family. Their recorded history also extends over a much longer period than that of the other twelve genera. Periechocrinus occurs first in the Niagara,—large, thin plated forms, nearly devoid of ornamentation, and having tall obconic calyces, with long arms branching one or more times. The evidence of this type in the American Devonian is as yet rather meager, though in Europe abundant testimony of its existence in rocks of similar age is not lacking. The forms found in the Lower Carboniferous present a somewhat different aspect from those of the earlier periods, having the calyx very much shortened and proportionately broadened at the base of the free arms, besides differing in several other respects.

On the other hand, Megistocrinus, with its thick, heavy plates, boldly sculptured, and having a very depressed calyx, reached its greatest development in the middle Devonian. It continued, though in greatly lessened numbers, to the upper part of the Burlington, where it became extinct. Both genera appear to have a larger number of dorsal interradials, especially on the anal side, than any other of the Actinocrinoid genera.

Amphoracrinus approaches Agaricocrinus in the flattened dorsal cup, the high, often inflated, ventral portions, and in the shape and arrangement of the plates of the aboral side. The anal side and arms connect it with Actinocrinus and Periechocrinus: with the former by the possession of usually only two ossicles in the second tier, by the absence of the marked vertical row of anal plates, and by the presence of a short sub-central anal tube; with the latter by the peculiar structure of the free arms.

Agaricocrinus is remarkable for the greatly depressed form of the calyx, the dorsal cup being nearly flat, or, as in some of the later species, decidedly concave. Its resemblance to Amphoracrinus has been referred to above. In anal structure it is identical with Dorycrinus, having the same arrangement of plates, and a similar vertical rounded ridge near the top of which is the simple anal opening. The arms are exceedingly stout, somewhat like those in certain forms of Actinocrinus from the lower part of the Burlington limestone, but very much heavier. Agaricocrinus, Amphoracrinus, and Dorycrinus probably began to diverge from the more typical members of the family and from each other about the same time, and this apparently took place during the middle or lower Devonian. In the upper part of the Burlington or early Keokuk a small group of forms departed somewhat from the typical species. These have been placed under Alloprosallocrinus, though it is doubtful whether the differences are great enough to render a separate generic term useful. The chief point of distinction is the position of the anal opening, which is placed at the end of a short ventral tube, instead of being a simple aperture in the test, as in Agaricocrinus. It seems, however, that much more importance has been hitherto

PLATE VII.


AMERICAN ACTINOCRINIDÆ
CARBONIFEROUS.
DEVONIAN.
SILURIAN.
UPPER.
LOWER.
Coal-Measures.
Kaskaskia.
St. Louis.
Keokuk.
Burlington.
Kinderhook.
Upper.
Middle.
Lower.
Upper.
Lower.
Periechocrinus
Megistocrinus
Amphoracrinus
Allopresallocrinus
Agaricocrinus
Dorycrinus
Gennaeocrinus
Erythrocrinus
Batocrinus
Actinocrinus
Pleiocrinus
Physetocrinus
Strotocrinus
Steginocrinus

placed upon this structure in classification than it probably deserves, as will be referred to later.

Dorycrinus is directly traceable to a certain group of Devonian crinoids for which the name Gennæocrinus has been proposed. The latter genus embraces a few small forms, mostly from the Hamilton rocks. The species of Gennæocrinus, as for example *G. cassedayi* Lyon, are connected with Burlington and later Dorycrinus by such forms as lately have been found in the Kinderhook beds of Central Iowa, and which have been described by Wachsmuth and Springer as *D. immaturus* and *D. parvibasis*. Dorycrinus, in combining the features of both, unites closely the Batocrinoid and Agaricocrinoid groups. It agrees with the first in the peculiar construction of the posterior side, in the simple anal opening, and in the radial grouping of the arms; with the second in the shape and structure of the calyx, and in the somewhat flattened distal portions of the arms, in this respect approaching certain Eretmocrini. In the earlier, more generalized forms the close resemblance of Dorycrinus, Agaricocrinus and Eretmocrinus or Batocrinus is far more striking than with later varieties which have become so greatly differentiated. The most prominent features, perhaps, to be noted in this connection are the monstrous ventral spines, often reaching a length of three to five inches, as in *D. mississippiensis* Roemer, and *D. roemeri* M. and W.; the immense basal expansion, as shown by *D. missouriensis* (Shumard) and *D. cornigerus* (Hall); and the stout, heavy stalks with large, conspicuous nodal joints.

Eretmocrinus differs from its nearest related genus—Batocrinus—of which it is manifestly an offshoot, chiefly in having long, flattened, lanceolate arms, a somewhat different ventral structure, and usually a more or less well defined lateral extension of the basals. The genus was rather short-lived, appearing in the Burlington and becoming extinct before the close of the Keokuk.

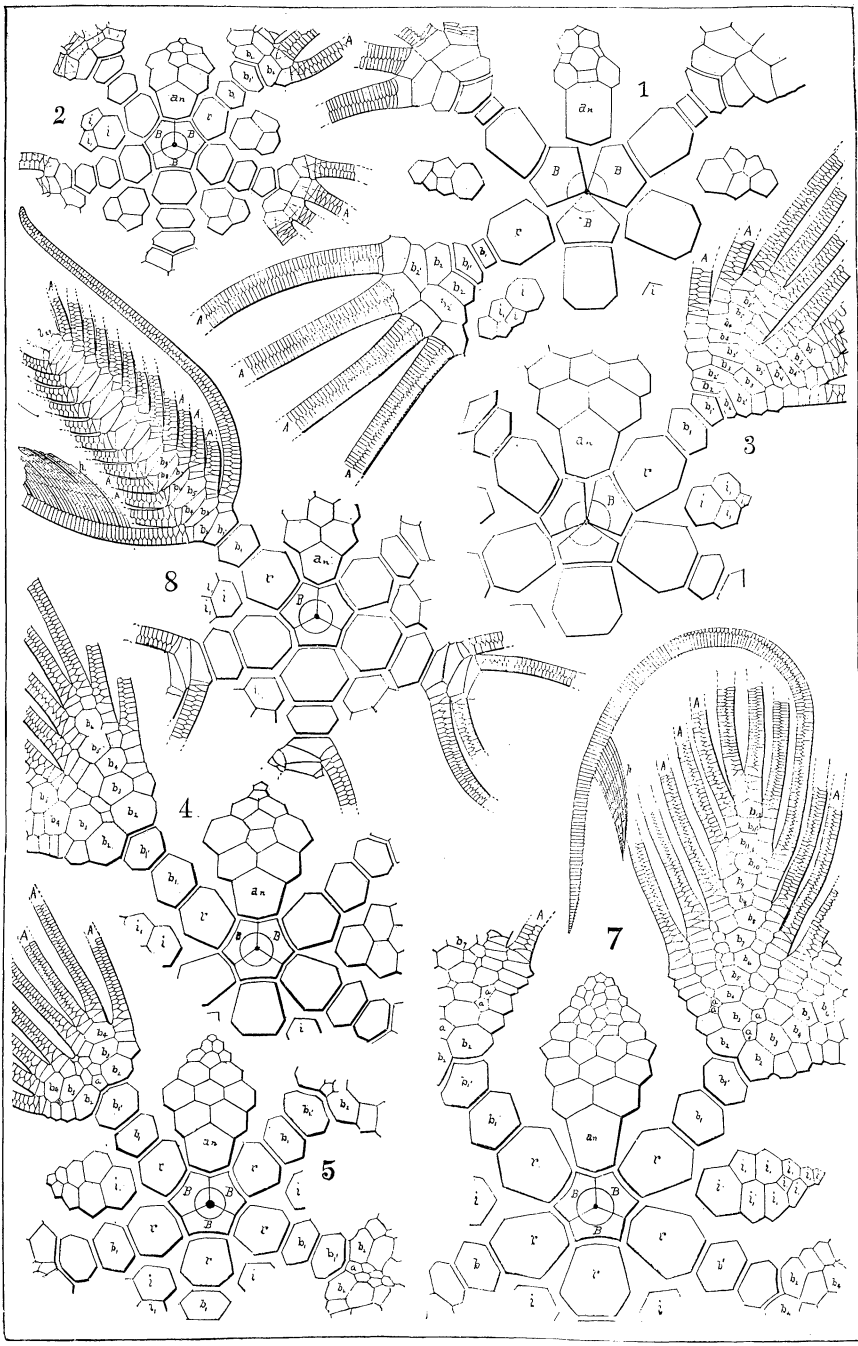
Batocrinus is one of the most characteristic and widely spread forms of the family occurring in the lower Carboniferous. Its relations to the other genera have already been considered elsewhere and need not be repeated here.

Actinocrinus is the type of a most remarkable group. The earlier forms bear a close resemblance to those of Batocrinus, but the possession of only two plates in the second anal tier serves readily to distinguish the two genera. As yet it has not been found to occur below the Carboniferous. It early shows a marked tendency to differentiation along the radial lines, assuming most wonderful phases, which culminated in Teleiocrinus, Strotocrinus, and Steganocrinus. The more primitive forms of Actinocrinus have the free arms, as they leave the calyx, nearly at equal distances from one another, In certain species, however, the arms of one ray begin to separate from those of the adjoining rays. Interradial plates still further increase the distance between the clustered free arm bases of the several rays, until finally the calyx has become strongly quinquelobate. The first section gradually diminished in numbers and disappeared in the upper part of the Burlington; but the second continually grows more and more prominent, and ultimately attains huge dimensions before the extinction of the group.

In the upper portion of the Burlington appears a small group of crinoids—Teleiocrinus—possessing all the characters of Actinocrinus except that the lower branchials for some distance have become larger, and appear like calyx plates. These are all firmly anchylosed, and do not give off the fine biserial arms until the fifth or sixth order of brachials. The calyx thus possesses a more or less well-defined lateral extension passing around above the branchial of the second order. This has led to the union of this group with Strotocrinus; but the rim, though very striking and very similar in each, appears to be a separate development in the two genera, rather than different stages of the same feature. In the ornamentation, the ventral structure, and the possession of a very long anal tube the affinities of Teleiocrinus are manifestly much nearer the typical representative of the family than Strotocrinus.

The Physetocrinus type begins to make its appearance in the Kinderhook as a derivative of Actinocrinus. The earliest known divergence, perhaps, is shown best in *A. ornatissimus* W. and Sp. from the lowest member of the lower Carboniferous. In this

PLATE VIII.



AMERICAN ACTINOCRINIDÆ.

form the radial portions of the calyx have already commenced to become somewhat lobate, and the arms to grow longer and more slender. The plates of the ventral side are all quite small, the ovals indistinguishable from the surrounding ossicles; while the pieces around the anal tube are still smaller, indicating that this structure was very short, and in many cases probably did not project much above the ventral dome. The ornamentation of both also presents a close similarity. Some forms of *A. orpusculus* Hall, from the lower part of the Burlington limestone, also show the Physetocrinus facus, but in a much less merked degree Physetocrinus appears to be the line along which Strotocrinus developed into the unique, short-lived forms which are found only in the upper part of the Burlington.

With the calyx alone under consideration Steganocrinus would be immediately referred to Actinocrinus, but the immense, narrow, radial extensions from which spring the free arms are certainly distinctive enough for generic separation. Although in this character the genus, at first sight, departs so far from the other groups of the family, it will be seen on closer examination that the departure is only another phase of what is shown in Strotocrinus, a devergence beginning a little earlier and in a little different direction.

Summary. Several interesting points are disclosed in the foregoing sketch of the American Actinocrinidæ, which have an important bearing upon the consideration of fossil faunas in general. The conclusions here arrived at apply, in the main, to other families of crinoids as well as to the gastropods and other paleozoic forms, though not to so apparent an extent. Considerable information has already been obtained illustrating these phenomena in the groups last mentioned, and will be the subject of future reference.

(1.) It is clearly indicated that a large proportion of the genera date back much further geologically than actual observation shows.

(2.) At times in the phylogenetic history of a group variations appear to go on with broad and rapid strides, and the organisms survive through rapidly changing physical conditions.

When the changes of environment became too rapid, the forms either ceased, to exist or retrograded, became depauperate and finally extinct. Admirable illustrations are found in Batocrinns, Dorycrinus, and especially in the Hexacrinoid genus Dichocrinus.

(3.) Variation may go on in one portion of an organism without materially affecting other parts. This is well shown in Steganocrinus as compared with Actinocrinus, and among the the Platycrinidæ in Eucladocrinus and Platycrinus, in the Rhodocrinidæ by Gilbertsocrinus and Rhodocrinus.

(4.) The Actinocrinidæ show a decided tendency throughout their existence to increase the distal extent of the rays. In some forms it was accomplished by the simple branching of the free arms, as in Megistocrinus, certain Amphoracrini, and a few Actinocrini; by the lateral expansion of the arms, as in Eretmocrinus; or by radial extension of the calyx branchials, as, notably, in Teleiocrinus, Strotocrinus and Steganocrinus. The number of free arms was thus increased from twenty or thirty in the earlier species of Actinocrinus, to forty to sixty in Teleiocrinus, one hundred to one hundred and twenty-five in Strotocrinus, and from one hundred and fifty to two hundred in Steganocrinus.

Explanation of Figures.

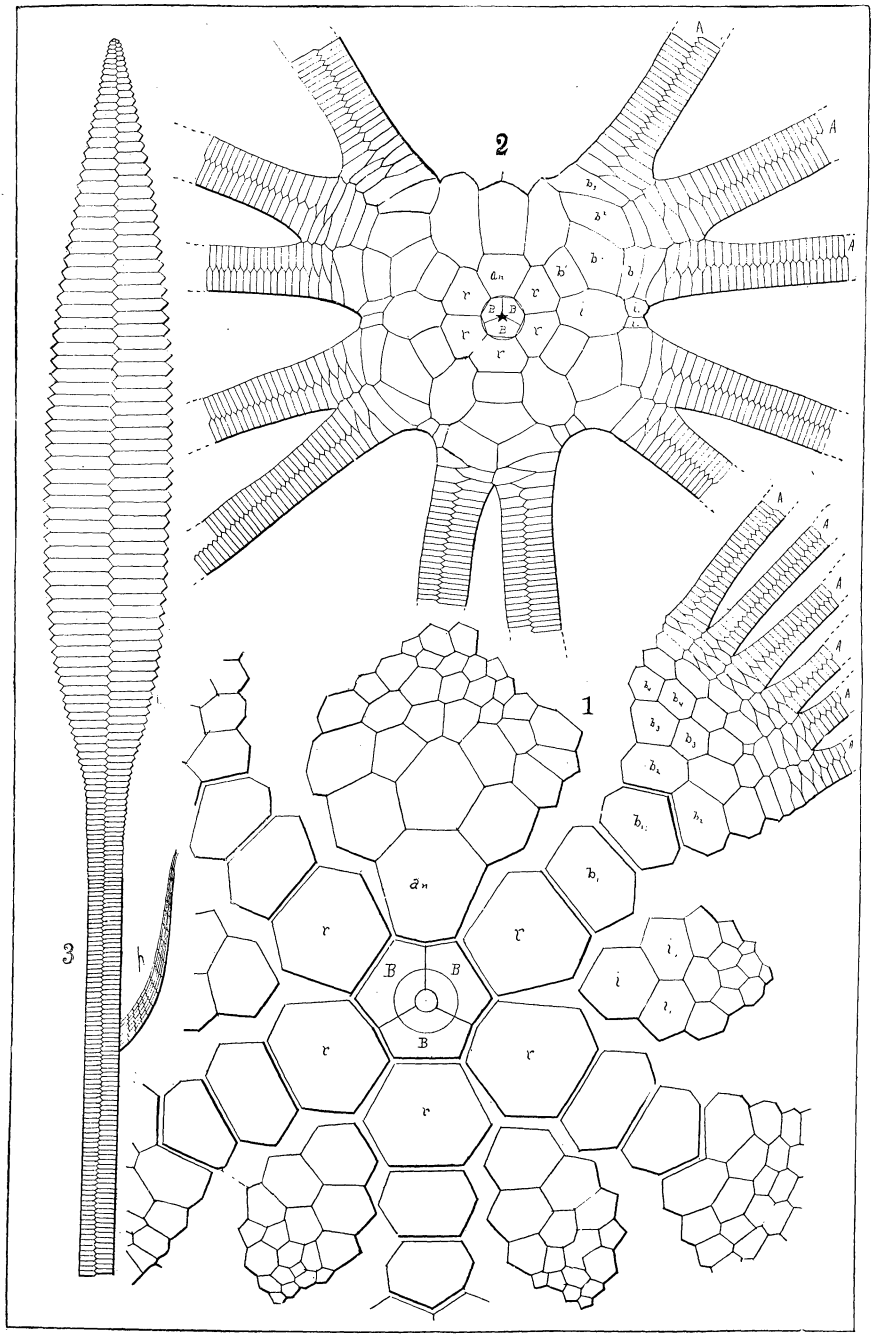
Plate VII.—Graphic representation of the generic relations and distribution in time of the American Actinocrinidæ.

Plate VIII.—Dorsal surfaces of Actinocrinidæ. *B*, basals; *r*, radials; *b*, branchials; *A*, free arms; *i*, interradials; *an*, primary anal plate; *p*, pinnucles; *a*, interaxillaries.

1. *Batocrinus pyriformis* (Shumard). 2. *Actinocrinus proboscidalis*, (Hall.) 3. *A. multiradiatus* (Shumard.) 4. *Teleiocrinus umbrosus* (Hall.) 5. *Physetocrinus ornatus* (Hall.) 7. *Strotocrinus regalis* (Hall.) 8. *Steganocrinus sculptus* (Hall.)

Plate IX.—1. *Megistocrinus evansi* (O. and Sh.) 2. *Agaricocrinus wortheni* (Hall.) 3. Free arm of *Eretmocrinus remibrachiatus* (Hall.)

PLATE IX.



American Actinocrinidæ.